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Multiple-scale interactions structure macroinvertebrate assemblages associated with kelp understory algae

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Abstract

Aim: Kelp forests provide habitat and food that supports a high diversity of flora and fauna. While numerous studies have described macroinvertebrates associated with kelp blades, stipes and holdfasts, a key kelp forest microhabitat, epilithic understory algae, remains poorly studied. Here, we used a macroecological approach and artificial seaweed units (ASUs) to explore the effects of ocean climate, wave exposure and habitat complexity on understory algal associated macroinvertebrate assemblages within *Laminaria hyperborea* forests in the United Kingdom.

Location: 9° latitudinal gradient along the north and west coasts of the United Kingdom.

Methods: Replicate ASUs comprising four different habitat complexities were deployed under mature *L. hyperborea* at 2 sites (along a wave exposure gradient, separated by km) within each of 4 locations (separated by 100s km) nested within two regions (warm and cold, spanning 9° of latitude). After 5 months in situ, the ASUs were collected and macroinvertebrates were identified to species level and enumerated.

Results: Habitat complexity and wave exposure both influenced macroinvertebrate assemblage structure, but results also showed clear effects of ocean climate, with macroinvertebrate assemblages differing between warm and cool regions, primarily driven by higher diversity and evenness in the warmer region and greater abundance in the cooler region.

Main conclusions: Predicted warming and a shift to less complex turf-forming algal assemblages are likely to alter the structure of macroinvertebrate assemblages associated with understory algae, with potential implications for kelp forest food web dynamics.

KEYWORDS

artificial seaweed units, climate change, kelp, *Laminaria hyperborea*, macroecology, macroinvertebrates, space-for-time, understory algae, wave exposure

1 | INTRODUCTION

Determining the composition of communities and understanding the processes that drive their structure are a central goal in ecology (Morin, 2011; Smith, Lyons, Ernest, & Brown, 2008). This, however, remains a major challenge given the multiple biotic and abiotic processes that may interact across varying spatiotemporal scales leading to the ecological patterns observed (Morin, 2011; Sutherland et al., 2013). In the marine realm, abiotic factors such as temperature (Kordas, Harley, & O'Connor, 2011), light (Lee, Park, & Kim, 2007), nutrients (Lee et al., 2007; Lobban & Harrison, 1997; Russell & Connell, 2005), hydrodynamics (Burrows, Harvey, & Robb, 2008; Graham et al., 1997; Raffaelli & Hawkins, 1999) and topography (Archambault & Bourget, 1996; Toohey & Kendrick, 2008) all play a major role in shaping communities.

Marine communities are structured across multiple spatial scales, and it is important to take these into consideration when exploring the underlying processes driving observed ecological patterns (Robuchon, Valero, Thiébaut, & Le Gall, 2017). At large spatial scales, temperature is considered to be a key determinant of biogeographic distributions of marine species (Somero, 2005; Southward, Hawkins, & Burrows, 1995; Sunday, Bates, & Dulvy, 2012; Tittensor et al., 2010; Waldock, Stuart-Smith, Edgar, Bird, & Bates, 2019). At small-to-moderate scales (i.e., 10 s m–10 s km), other factors such as hydrodynamic forces (Graham et al., 1997; Hiscock, 1983; Raffaelli & Hawkins, 1999; Sousa, 1984) and habitat complexity (MacArthur & MacArthur, 1961; Thompson, Wilson, Tobin, Hill, & Hawkins, 1996) can exert a strong influence on marine communities, influencing their structure (Smale & Moore, 2017). Marine organisms respond differently to wave-induced stress with some species adapted to high to moderate wave action (e.g., the kelp *Laminaria hyperborea* [Bekkby, Rinde, Erikstad, & Bakkestuen, 2009; Bekkby et al., 2019; Smale et al., 2016]) and others being more suited to sheltered conditions (e.g., the kelp *Saccharina latissima*, Bekkby & Moy, 2011; Kain, 1979; Parke, 1948). Habitat complexity also influences assemblage structure at mesoscales (<10 m; Cowles, Hewitt, & Taylor, 2009; MacArthur & MacArthur, 1961; Thompson et al., 1996). Highly complex habitats provide refuge from predation for a wide range of species (Gibbons, 1988; Holmlund, Peterson, & Hay, 1990; Martin-Smith, 1993) and offer protection from physical disturbance such as wave action (Fretter & Manly, 1977). As such, the abundance and diversity of marine invertebrate assemblages are generally greater in habitats that are structurally complex than in those that are more homogeneous (Cowles et al., 2009; Kovalenko, Thomaz, & Warfe, 2012; Thompson et al., 1996). At local scales (<1 m), patterns of assemblage structure can be influenced by a range of fine-scale abiotic and biotic processes, leading to high levels of local-scale variability (Irving, Connell, & Gillanders, 2004; Leclerc, Riera, Lévêque, & Davoult, 2016).

Covering 25% of global coastlines, kelps (large brown seaweeds in the order Laminariales) are the dominant canopy-forming macroalgae found on temperate shallow rocky reefs (Steneck et al., 2002; Wernberg, Krumhansl, Filbee-Dexter, & Pedersen, 2019). The complex biogenic structure formed by many kelp species provides a three-dimensional habitat which modifies the surrounding environment by altering light levels, water motion and sedimentation rates (Bennett et al., 2015; Eckman, Duggins, & Sewell, 1989; Moore, 1972; Wernberg, Kendrick, & Toohey, 2005; Wing & Patterson, 1993). Similar to terrestrial forests, kelp forests are characterized by a dense canopy that can facilitate the growth and survival of a wide variety of understory algae (Bennett et al., 2015; Leclerc et al., 2015, 2016; Norton, Hiscock, & Kitching, 1977), many of which would not be present without kelp (Graham, 2004; Norton et al., 1977). This algal understory algae in turn provides food and shelter for macroinvertebrates that in turn become resources for higher trophic levels, including fish and marine mammals (Christie, Jørgensen, Norderhaug, & Waage-Nielsen, 2003; Norderhaug, Christie, Fosså, & Fredriksen, 2005; Pérez-Matus et al., 2012; Teagle, Hawkins, Moore, & Smale, 2017). Kelp forests are therefore recognized as one of the most productive and diverse habitats on Earth (Mann, 1973), and kelps are considered "true" ecosystem engineers (sensu Jones, Lawton, & Shachak, 1994).

To date, most research on the structure of kelp-associated microhabitats has tended to focus on diversity found on kelp stipes and stipe-associated epiphytes (Anderson, Rothman, Share, & Drummond, 2006; Christie et al., 2003; Lippert, Iken, Rachor, & Wiencke, 2001; Włodarska-Kowalczuk, Kukliński, Ronowicz, Legeżyńska, & Gromisz, 2009) as well as within kelp holdfasts (Raffo, Eyras, & Iribarne, 2009; Ríos, Arntz, Gerdes, Mutschke, & Montiel, 2007; Smith, Simpson, & Cairns, 1996; Teagle, Moore, Jenkins, & Smale, 2018). However, a diverse and abundant, but less studied, macrofaunal assemblage is associated with the epilithic understory algal assemblages found beneath the kelp canopy (Schaal, Leclerc, Droual, Leroux, & Riera, 2016 but see meiofauna: Arroyo, Maldonado, Pérez-Portela, & Benito, 2004; macrofauna: Leclerc et al., 2016). These epilithic algal assemblages are dominated by red algae (Benes & Carpenter, 2015; Johnson & Mann, 1988; Leclerc et al., 2016; Leliaert, Anderson, Bolton, & Coppejans, 2000; Maggs, 1986) and consist of perennial, pseudo-perennial and annual species which can be diverse and structurally complex (Clark, Edwards, & Foster, 2004; Flukes, Johnson, & Wright, 2014; Maggs, 1986; Norton et al., 1977; Steneck & Dethier, 1994). As with epiphytic algae (Christie, Jørgensen, & Norderhaug, 2007), the heterogeneity of epilithic algae is believed to provide habitat and food for a wide range of organisms that in turn become resources for higher trophic levels (Christie et al., 2003; Norderhaug et al., 2005; Pérez-Matus et al., 2012; Teagle et al., 2017). Importantly, the faunal assemblages associated with epilithic algae may be different to those associated with kelp and kelp epiphytes (Christie et al., 2003; Leclerc et al., 2015, 2016). Given the significant role that epilithic algal communities may play in terms of kelp forest secondary production, it is important to include these habitats in our wider understanding of the structure and functioning of these ecosystems.

Understanding the structure and functioning of kelp forest ecosystems is particularly important as across the globe they are being impacted by multiple stressors including ocean warming (Filbee-Dexter,

Feehan, & Scheibling, 2016; Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012; Voerman, Llera, & Rico, 2013; Wernberg et al., 2016), eutrophication (Airoldi & Beck, 2007; Gorgula & Connell, 2004; Gorman & Connell, 2009; Norderhaug et al., 2015) and overexploitation (Airoldi & Beck, 2007; Coleman & Williams, 2002; Steneck et al., 2002). Ocean warming (both decadal scale and marine heatwaves) has led to the redistribution of species ranges (Smale, 2019; Tuya et al., 2012; Wernberg et al., 2016) and along with other stressors (see Filbee-Dexter & Wernberg, 2018) a switch from complex kelp-dominated environments to low structural complexity and at times functionally depauperate turf habitats (Filbee-Dexter & Wernberg, 2018). With 38% of global kelp forests in decline (Krumhansl et al., 2016), it is important for the management and conservation of these ecosystems that we understand the structure and drivers of that structure for all components of these highly diverse and productive ecosystems.

In the NE Atlantic, shallow subtidal reefs, fully or partially exposed to wave action, are dominated by the large stipitate kelp *Laminaria hyperborea* (Smale, Burrows, Moore, O'Connor, & Hawkins, 2013; Steneck et al., 2002; Teagle et al., 2017). Individual "plants" support diverse assemblages of epiphytic algae and associated invertebrates on their stipes, as well as rich invertebrate assemblages within their holdfasts (Christie et al., 2003; Moore, 1973; Teagle et al., 2017, 2018). Beneath these, extensive kelp stands lie functionally diverse and structurally complex assemblages of understory algae, ranging from simple foliose species to more complex calcareous algae and corticated macrophytes (Leclerc et al., 2016; Maggs, 1986). These in turn provide habitat for a range of macroinvertebrates (Leclerc et al., 2016; Schaal et al., 2016), yet there is currently limited information about the structure and drivers of variation in macroinvertebrate assemblages associated with kelp understory epilithic algal assemblages.

Understanding the structure and functioning of kelp forest ecosystems at multiple spatial scales is vital to anticipate and mitigate against future changes related to stressors such as climate change, anthropogenic driven phase shifts, pollution and overfishing. Here, we used an experimental macroecological approach to investigate: (a) the structure and variability of macroinvertebrate assemblages associated with artificial epilithic understory algal assemblages within *L. hyperborea* forests situated along a 9° latitudinal gradient; (b) the potential drivers leading to the observed variability in ecological patterns; and (c) by using a space-for-time gradient as a proxy for future ocean warming provide some insight into how epilithic understory algal assemblages might be structured into the future.

2 | METHODS

2.1 | Study area

The study was conducted across two thermal regions (cold and warm), which spanned 9° of latitude (~50° to ~59°N), within which temperature variations were highly consistent across locations and represented a well-established and characterized average temperature gradient of ~2.5°C (Smale et al., 2016; Smale & Moore, 2017). Within the context of a "space-for-time" substitution approach, the gradient encompasses end of the century predictions for warming in this region (Philippart et al., 2011). Two sites were established within each of four locations (northern Scotland (mean (±*SE*) temperature during experiment: 11.7°C ± 0.02), western Scotland (11.9°C ± 0.01), southwest Wales: (14.2°C ± 0.01) and southwest England (14.7°C ± 0.01)) which were nested within the two thermal regions (Figure 1). Study sites within each location were selected to represent high wave exposure (1.02 m/s (north Scotland), 0.22 m/s (western Scotland), 0.73 m/s (southwest Wales), 0.42 m/s (southwest England)) and moderate wave exposure (0.30 m/s [northern Scotland], 0.08 m/s [western Scotland], 0.34 m/s [southwest Wales], 0.22 m/s [southwest England]; Smale et al., 2016). The study area was unconfounded by environmental factors such as tidal movement, water clarity, nutrient levels and grazing pressure, which were broadly comparable across locations, and sites were unaffected by localized stressors (e.g. sewage outfalls, fish farms; Smale et al., 2016; Smale & Moore, 2017).

2.2 | Artificial seaweed units

In order to control for differences in assemblage structure that commonly occur across macroecological scales (Irving et al., 2004), we used artificial seaweed units (ASUs) modelled on algal functional groups (sensu Steneck & Dethier, 1994). A functional approach was considered appropriate as studies within kelp forests have shown macrofauna are more likely to associate with specific habitat structure or functional groups over particular algal species (Christie, Norderhaug, & Fredriksen, 2009; Hacker & Steneck, 1990; Norderhaug, Christie, Andersen, & Bekkby, 2012). The ASU approach was also considered advantageous as it allowed for control of settlement period of macroinvertebrates and habitat complexity (Norderhaug, Christie, & Rinde, 2002), as well as ensuring that palatability of specific algal species was not driving the assemblage patterns observed (Norderhaug et al., 2002). ASUs have previously been used to investigate macrofaunal assemblage structure associated with Laminarian epiphyte assemblages and holdfasts across smaller spatial scales (Christie et al., 2007; Hauser, Attrill, & Cotton, 2006; Norderhaug et al., 2002; Walls, Edwards, Firth, & Johnson, 2017). In total, four ASUs of different complexity were created as follows: finely branched (3D fractal dimension: $D = 2.756$); corticated ($D = 2.321$); foliose ($D = 2.191$); and articulated calcareous algae (ACA; $D = 2.468$; Table S1). Each ASU was attached to a PVC panel (15 × 15 cm) using cable ties and then attached to a concrete slab (60 × 60 cm) via screws and rawl plugs. Each slab contained an identical set of four ASUs (Figure S2).

2.3 | Sampling

In May 2016, ASUs were placed within mature stands of *Laminaria hyperborea* forest (~2–4 m below chart datum; Smale et al., 2016)

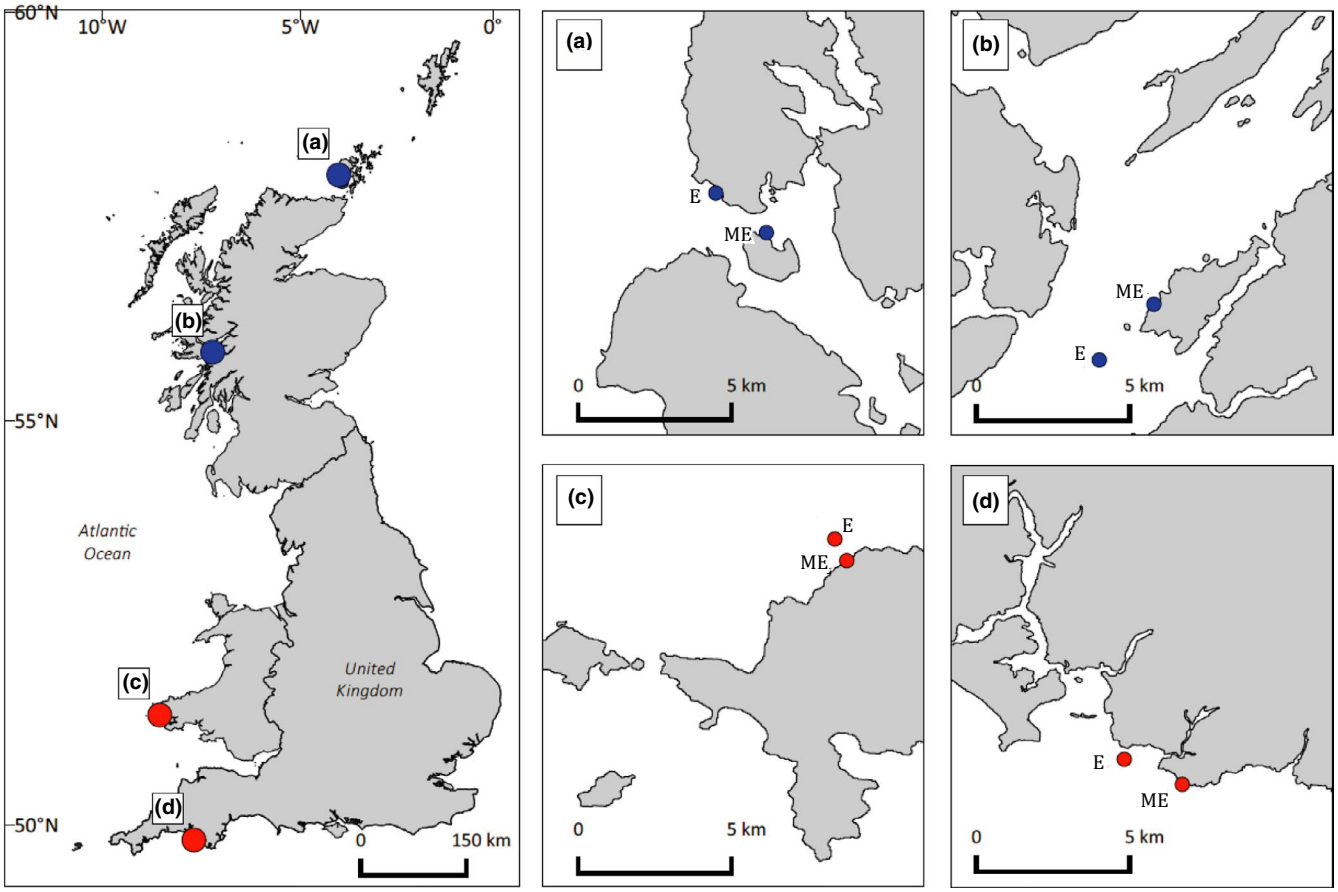

FIGURE 1 Four study locations nested within two thermal regimes (cold: northern Scotland (a), western Scotland (b); warm: southwest Wales (c), southwest England (d)). Smaller maps indicate the two study sites within each location with E representing the exposed site and ME the moderately exposed site

at the eight study sites described above. Three concrete slabs and therefore three replicates of each ASU were deployed at each site. After five months, ASUs were recovered by scuba divers by placing a cotton bag over each ASU, to ensure mobile species were retained, prior to cutting the ASU free and sealing the bags underwater. In the laboratory, macrofauna were removed from ASUs by washing them over a 500-μm sieve. Retained macrofauna were preserved in 70% industrial methylated spirit (IMS) and later identified down to the finest level of taxonomic resolution possible (i.e., mostly species level with the exception of polychaetes which were identified to family level, nemertean to phylum level and some female amphipods to family level as males are required to get to species level, e.g. Aoridae). All individuals were then enumerated.

2.4 | Statistical analyses

Both univariate and multivariate analyses were conducted using PRIMER v7 software (Clarke & Gorley, 2015) with the PERMANOVA add on (Anderson, Gorley, & Clarke, 2008). Prior to all analyses, data were first standardized by ASU volume to account for variability in habitable space. To examine the relationship between assemblage structure and ASU complexity, fractal dimension was included as a covariate in all analyses. Initial analyses included slab as blocking factor, but this was found to be insignificant as a main effect ($p = .319$), and there was no significant interaction with other factors in our statistical model ($p > .05$, Table S3 and S4). Given the complexity of the statistical model, slab was removed from the model to improve clarity (Quinn & Keough, 2002). Variability in macroinvertebrate assemblage structure was examined using a 4-factor PERMANOVA with the model comprising region (fixed, 2 levels), location (fixed, 4 levels and nested in region), wave exposure (fixed, 2 levels) and ASU type (fixed, 4 levels) on fourth-root transformed data to down weight the importance of numerically dominant taxa such as amphipods. Permutations (9,999 under a reduced model) were based on a Bray–Curtis similarity matrix. Pairwise tests were performed wherever significant differences were detected ($p < .05$). To determine which taxa contributed the most to the observed dissimilarities, a similarity percentage procedure (SIMPER) was carried out. Patterns in macroinvertebrate assemblage structure were visualized using non-metric multidimensional scaling (nMDS). Diversity measures included species richness S, faunal abundance N, $\log_e$-based Shannon diversity index H' (Shannon & Weaver, 1963) and Pielou evenness J' (Pielou, 1966). These univariate metrics were examined using the same permutation-based model described above but with matrices based on Euclidian distance. Prior to analysis, homogenous

dispersion around the centroid was checked for all factors using the PERMDISP routine. Where significant differences in dispersion existed, the critical threshold of significance was modified to be more conservative ($p < .01$). Significant terms were examined further via pairwise comparisons.

3 | RESULTS

A total of 76,481 individuals from 173 taxa (mostly species level) were identified with amphipods being the dominant group in terms of diversity and abundance, representing more than two thirds of the individuals enumerated (52,240 individuals, 45 taxa), followed by bivalves (12,410 individuals, 28 taxa), gastropods (5,964 individuals, 28 taxa) and polychaetes (1,579 individuals, 19 families). Other numerous taxa included decapods (1,492 individuals, 11 families), isopods (1,263 individuals, 10 taxa) and echinoderms (1,019 individuals, 10 taxa; see Table S5).

3.1 | Macrofaunal assemblage structure

There was variability in the proportion of taxa across sites, but in general there was a greater proportion of amphipods and bivalves in the cold region while decapods and polychaetes were found in greater proportions in the warm region (Figure 2a). For ASUs, there was a greater proportion of amphipods on foliose and corticated ASUs but a greater proportion of bivalves on finely branched and articulated calcareous algae (ACA) ASUs (Figure 2b). There was a significant relationship between fractal dimension and assemblage structure, indicating that ASU complexity was an important driver of the patterns observed (Table 1). The non-metric MDS plot (Figure 3) showed a clear separation between warm and cold regions, however, the PERMANOVA detected a significant three-way interaction between region, ASU type and wave exposure (Table 1). This significant higher-order interaction term was a result of non-significant differences in macroinvertebrate assemblages associated with foliose ASUs at exposed and moderately exposed sites in the warm region and non-significant differences associated with foliose and ACA ASUs at exposed sites in the cold region and at moderately exposed sites in the warm region (Table S6). When comparing between warm and cold regions, irrespective of wave exposure, macroinvertebrate assemblage structure was different across all ASU types (Table S6). In general, the dissimilarity in assemblage structure between warm and cold regions was diffusely spread across a number of taxa (Table S7). There were, however, some clear patterns. The amphipods *Jassa-Ischyrocerus* spp., *Stenothoe* spp, the gastropod *Margarites helicinus* were either only present in the cold region or were found in higher abundances in this region (Figure 4). In contrast, the gastropod *Tricolia pullus*, the bivalve *Modiolus modiolus*, the

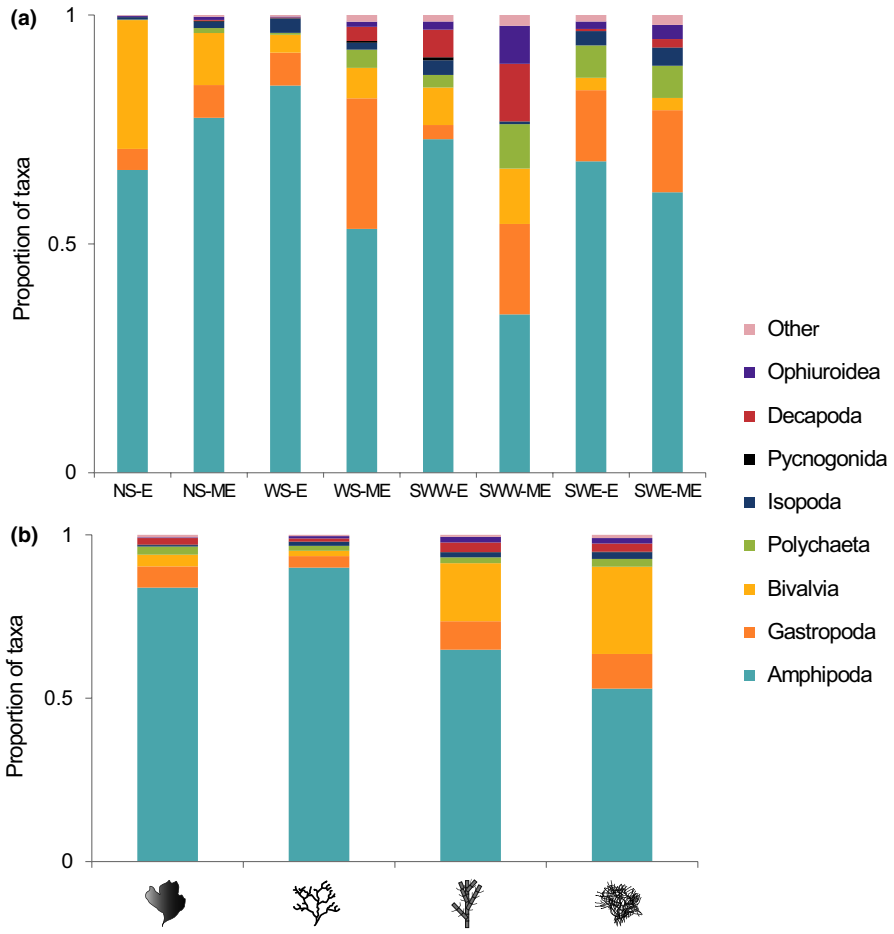

FIGURE 2 Proportion by individual count of major taxonomic groups associated with (a) site and (b) ASU types (left to right: foliose, ACA, corticated and finely branched ASUs). NS represents northern Scotland; WS western Scotland;SWW southwest Wales; and SWE southwest England, while E and ME represent wave-exposed and moderately exposed sites, respectfully

TABLE 1 Results of PERMANOVA test for differences in macroinvertebrate assemblage structure between region (fixed), location (nested in region, fixed), wave exposure (fixed) and ASU type (fixed)

Source	*df*	MS	Pseudo-*F*	*p*
Fractal dimension	1	15,889	19.068	**.0001**
Region	1	34,037	40.846	**.0001**
Location (Region)	2	17,909	21.492	**.0001**
Exposure	1	12,949	15.539	**.0001**
ASU	2	7,124.6	8.5499	**.0001**
Region × Exposure	1	6,255.4	7.5067	**.0001**
Region × ASU	3	2,417.6	2.9012	**.0001**
Exposure × ASU	3	1,442.1	1.7306	**.0011**
Location (Region) × Exposure	2	4,641.8	5.5703	**.0001**
Location (Region) × ASU	6	1,954.4	2.3454	**.0001**
Region × Exposure × ASU	3	1,353.7	1.6245	**.0042**
Location (Region) × Exposure × ASU	6	928.3	1.114	.2329
Residual	60	833.31		
Total	91			

Note: Fractal dimension was included as a covariate in the analysis. Permutations (9,999) were conducted under a reduced model and were based on a Bray–Curtis similarity matrix of standardized (by volume), fourth-root transformed data. Significant values are indicated in bold. Significance was accepted at $p < .05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative *p*-value was adopted ($p < .01$). Underlined *p*-values indicate where main factors returned significant differences in within-treatment dispersion.

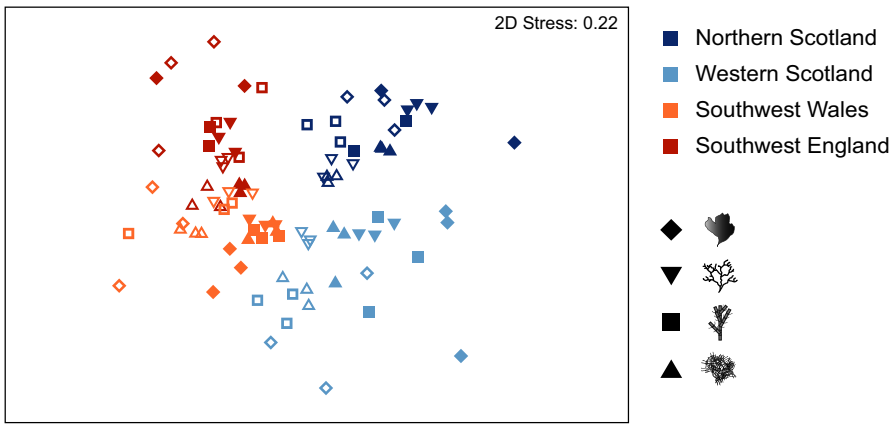

FIGURE 3 Non-metric MDS plot of macroinvertebrate assemblage structure across regions, locations nested within regions, wave exposure and ASU types. Symbols represent individual ASUs (bottom to top: finely branched, ACA, corticated and foliose ASUs) with blue shades representing the cold region, red shades the warm region, filled symbols represent exposed sites, and open symbols moderately exposed sites. Data were standardized by volume and fourth-root transformed, and similarities were based on Bray–Curtis similarity

decapod *Pisidia longicornis*, the amphipods *Gammaropsis maculata*, Aoridae, and the polychaete Nereididae were either only found in the warm region or in greater abundance in this region (Figure 4).

Differences in assemblage structure between exposed and moderately exposed sites were found in both regions and for all ASU types with the exception of the foliose ASU in the warm region (Table S6). The taxa driving these differences in both regions and across ASU groups included the amphipods *Jassa-Ischyrocerus* spp., *Gammaropsis maculata*, *Stenothoe* spp., which were found in greater abundance at exposed sites and the decapod *Pisidia longicornis* and the amphipod Aoridae, which were more frequently found at moderately exposed sites. (Figure 4).

For both region and wave exposure, assemblages from ASU types differed from each other (Table S6), with the exception of foliose and ACA ASUs at cold, exposed sites, and warm, moderately exposed sites. In general, there was a higher abundance of amphipods Caprellidae (e.g., *Caprella linearis*, *C. penantis*, *C. acanthifera and Phtisica marina*) on corticated ASUs compared to other ASU types.

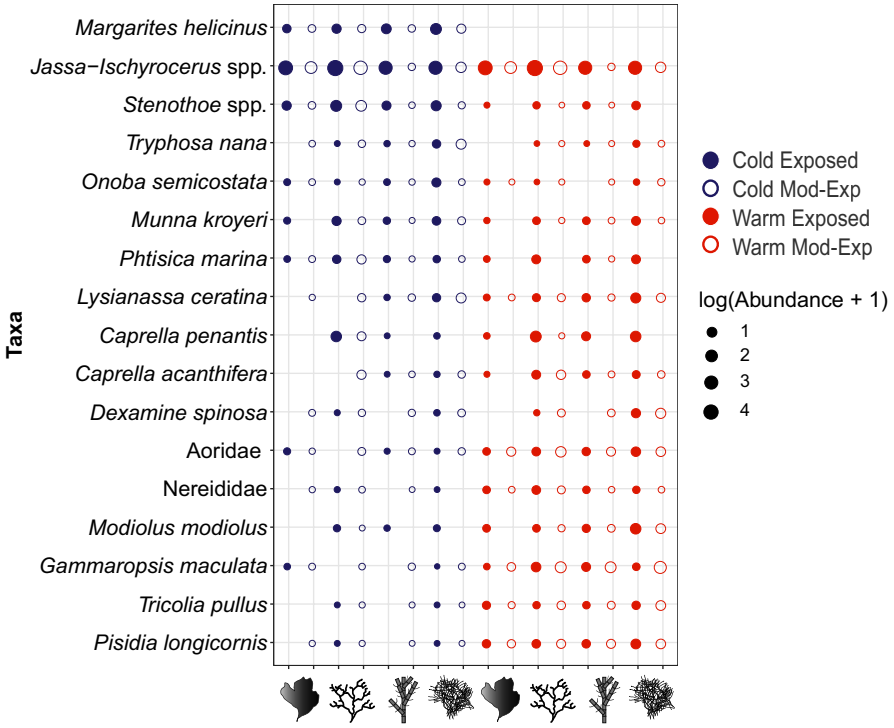

FIGURE 4 Major taxa contributing to the average dissimilarity between macroinvertebrate assemblages across regions, wave exposure and ASU type as determined by SIMPER analyses based on fourth-root transformed data. Bubble size indicates relative abundances (log + 1 transformed) of taxa for each ASU after standardization (by volume) (left to right: foliose, corticated, ACA and finely branched ASUs). The colour of the circle represents the region with cold region indicated by the blue shade and warm region indicated by the red shade. Filled circles represent exposed sites, and open circles moderately exposed sites (see Table S4 for full SIMPER results)

The bivalves *Modiolus phaseolina*, *M. costulatus* and *M. modiolus*, the gastropod *Onoba semicostata*, the isopod *Munna kroyeri* and the amphipods *Dexamine spinosa*, *Lysianassa ceratina* and *Tryphosa nana* were found in greater abundance on more complex structures (e.g. finely branched ASUs; Figure 4).

3.2 | Macrofaunal abundance and diversity

ASU complexity had no effect on macrofaunal abundance, however, there was a significant interaction between region, ASU type and wave exposure (Table 2a). Abundance was significantly higher in the cold region compared to the warm region at exposed sites, with the exception of foliose ASUs where abundance was similar across regions (Figure 5a; Table S8). There was little difference in abundance between regions at moderately exposed sites with the exception of foliose ASUs where abundance was significantly higher in the cold region (Figure 5a). In the cold region, abundance was greater at exposed sites than moderately exposed sites for all ASU types with the exception of foliose ASUs where no difference was observed. Exposure had no effect on abundance in the warm region. The exception to this was finely branched ASUs where abundance was higher at exposed sites (Figure 5a).

Taxon richness significantly increased with ASU complexity (Table 2b; Figure 6b). There was an interaction between location nested within region, wave exposure and ASU type (Table 2b). The nested effect was limited to specific ASU types. For example, taxon richness was higher in northern Scotland compared to western Scotland at moderately exposed sites for finely branched ASUs, but not significantly different elsewhere (Table 2b; Figure 5b; Table S9). For foliose ASUs, taxon richness was higher at the moderately exposed site compared to the exposed site in western Scotland, but not significantly different elsewhere (Figure 5b). There was no nested effect for ACA and corticated ASUs, with post hoc tests indicating that taxon richness in corticated ASUs was greater at moderately exposed sites in the cold region and differed between regions with greater taxon richness in the warm region at exposed sites but greater richness in the cold region at moderately exposed sites (Figure 5b). There was no difference in taxon richness for ACA ASUs across regions or wave exposure. Overall, finely branched and corticated ASUs supported the highest number of taxa while the least complex ASUs (e.g. foliose ASUs) supported the lowest (Figure 5b).

Diversity significantly increased with ASU complexity, while evenness did not (Table 2c,d; Figure 6c,d). There was a significant interaction between region and wave exposure for diversity H' and evenness J' (Table 2c,d). Diversity and evenness were higher in the warm region for all wave exposures and at moderately exposed sites for the cold region (Figure 5c,d; Tables S10 and S11). For diversity, there was also a significant interaction between wave exposure and ASU type (Table 2c) with greater diversity at moderately exposed sites for all ASU types with the exception of foliose ASUs where no differences were detected (Figure 5c). For evenness, an interaction between region and ASU type was found (Table 2d) with assemblages in the warm region more evenly distributed than in the cold region for all ASU types (Figure 5d). In the cold region, macroinvertebrates in corticated ASUs were less evenly distributed and diverse than in finely branched and ACA ASUs (Figure 5d). In the warm region, macroinvertebrates in foliose and ACA ASUs were more evenly distributed than in finely branched and corticated ASUs (Figure 5d).

TABLE 2 Results of univariate PERMANOVA tests for differences in macrofaunal abundance (a), taxon richness (b), diversity H' (Shannon–Wiener) (c) and evenness J' (Pielou) (d) between regions (fixed), locations (nested in region, fixed), wave exposure (fixed) and ASU type (fixed)

Source	*df*	MS	*F*	*p*	*df*	MS	*F*	*p*
	(a) Abundance				**(b) Taxon Richness**			
Fractal dimension	1	112	0.25541	.6236	1	9,701.6	713.79	**.0001**
Region	1	20,532	46.819	**.0001**	1	141.26	10.393	**.0032**
Location (Region)	2	14,790	33.727	**.0001**	2	57.633	4.2403	**.0205**
Exposure	1	24,318	55.454	**.0001**	1	72.99	5.3702	**.021**
ASU	2	12,861	29.329	**.0001**	2	1,922.6	141.45	**.0001**
Region × Exposure	1	13,377	30.504	**.0001**	1	158.1	11.632	**.001**
Region × ASU	3	4,766.9	10.87	**.0001**	3	98.325	7.2342	**.0007**
Exposure × ASU	3	1,617.3	3.688	**.0137**	3	131.59	9.6814	**.0001**
Location (Region) × Exposure	2	4,613.1	10.519	**.0003**	2	57.216	4.2097	**.0222**
Location (Region) × ASU	6	972.45	2.2175	**.0463**	6	30.72	2.2602	.052
Region × Exposure × ASU	3	1,248.8	2.8477	**.0432**	3	30.142	2.2177	.094
Location (Region) × Exposure × ASU	6	129.64	0.29563	.9392	6	45.944	3.3803	**.0064**
Residual	60	438.53			60	13.592		
Total	91				91			
	(c) Shannon–Wiener diversity				**(d) Pielou's evenness**			
Fractal dimension	1	7.8597	65.189	**.0001**	1	0.012363	0.78476	.3842
Region	1	10.431	86.519	**.0001**	1	0.96035	60.961	**.0001**
Location (Region)	2	1.2539	10.4	**.0001**	2	0.1656	10.512	**.0001**
Exposure	1	5.6348	46.736	**.0001**	1	0.49899	31.675	**.0001**
ASU	2	0.20675	1.7148	.1938	2	0.084411	5.3582	**.0071**
Region × Exposure	1	3.2694	27.116	**.0001**	1	0.26077	16.553	**.0001**
Region × ASU	3	0.26238	2.1762	.1008	3	0.076129	4.8325	**.0026**
Exposure × ASU	3	0.36014	2.987	**.0369**	3	0.015223	0.96634	.4298
Location (Region) × Exposure	2	0.17045	1.4137	.2538	2	0.014714	0.93401	.4071
Location (Region) × ASU	6	0.20068	1.6644	.1407	6	0.009124	0.57919	.751
Region × Exposure × ASU	3	0.048315	0.40073	.7573	3	0.004193	0.26619	.857
Location (Region) × Exposure × ASU	6	0.085851	0.71205	.6382	6	0.003582	0.2274	.9684
Residual	60	0.12057			60	0.015754		
Total	91				91			

Note: Fractal dimension was included as a covariate in the analysis. Permutations (9,999) were conducted under a reduced model and were based on a Euclidean distance similarity matrix of standardized (by volume) untransformed data. Significant values are indicated in bold. Significance was accepted at $p < .05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative p-value was adopted ($p < .01$). Underlined p-values indicate where main factors returned significant differences in within-treatment dispersion.

4 | DISCUSSION

Our study showed that both habitat complexity and wave exposure influenced macroinvertebrate assemblage structure. Clear effects of ocean climate were, however, detected, with macroinvertebrate assemblages differing between warm and cool regions, primarily driven by higher diversity and evenness in the warmer region and greater abundance in the cooler region.

Faunal assemblages associated with kelp stipes and holdfasts have received considerable attention and have been shown to be typically rich and diverse (Christie et al., 2007; Teagle et al., 2017, 2018), representing an important food source for consumers at higher trophic levels (Norderhaug et al., 2005). While some research on macrofaunal assemblages associated with understory epilithic algae has been conducted (meiofauna: Arroyo et al., 2004; macrofauna: Leclerc et al., 2016; Schaal et al., 2016), our study is

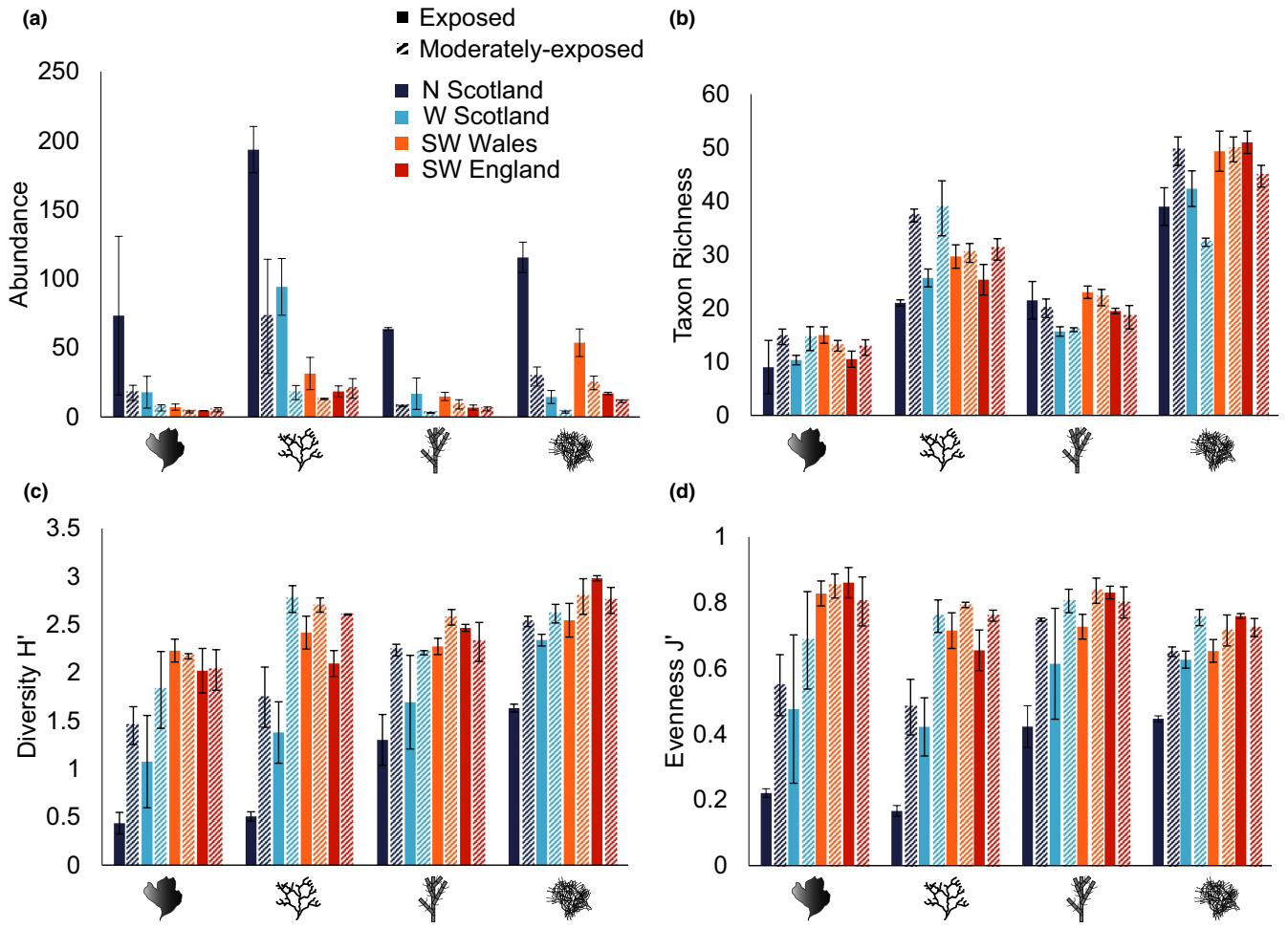

FIGURE 5 Mean (±*SE*) macrofaunal abundance (a), taxon richness (b), diversity (Shannon–Wiener *H′*) (c) and evenness (*J′* Pielou) (d) associated with ASU types (left to right: foliose, corticated, ACA and finely branched ASUs). The cold region is represented by blue shades and the warm region by red shades. Filled bars represent exposed sites and hatched bars moderately exposed sites. All measures of diversity are standardized by ASU volume

the first to investigate patterns of macroinvertebrate assemblages across macroecological scales. While using ASUs, to allow standardization across the broad spatial scale studied, the macroinvertebrates found associated with our ASUs are comparable to those found associated with natural understory algal assemblages (P. J. Moore, unpublished data). We therefore believe our results to be representative of what would be found in natural understory algae.

We found that artificial understory algae supported a rich and diverse macroinvertebrate assemblage consisting of 3 to 54 taxa (a total of 173 taxa across all 92 units) and 18 to 6,788 individuals per ASU (76,481 individuals across all 92 units). While not directly comparable due to differences in habitable area, these values are comparable to those reported for kelp holdfasts sampled along the same study gradient with a total of 187 taxa from 72 holdfasts (Teagle et al., 2018) and other studies of *L. hyperborea* holdfasts (27–89 species) and stipes (29–69 species; Teagle et al., 2017). While receiving limited attention previously, our study and Leclerc et al. (2015) suggest that macroinvertebrate assemblages associated with understory algae should be included in estimates of kelp forest secondary productivity and are likely to play an important role in coastal marine food webs.

The fauna found in our study were typical of fauna associated with kelp holdfasts (Teagle et al., 2017, 2018) with the exception that there were twice as many bivalve species in our ASUs (28 species for ASUs and 12 for holdfasts; Teagle et al., 2017, 2018). While some habitat fidelity has been noted for some taxa associated with epiphytic algae and holdfasts (Christie et al., 2003; Norderhaug et al., 2002), this relationship often breaks down (Norderhaug et al., 2002) as most species are highly mobile (Bartsch et al., 2008; Jørgensen & Christie, 2003). Similarities between taxa associated with holdfasts and ASUs investigated along the same large-scale gradient are therefore not a surprise and likely a result of individuals moving between habitats. Such movement between habitats is frequent (Jørgensen & Christie, 2003; Norderhaug et al., 2002) and provides predatory opportunities for fish and other consumers (Norderhaug et al., 2005). As a consequence, macroinvertebrates are a key link between primary production and higher trophic levels and, thus, play a crucial role in the transfer of energy and carbon within coastal food webs (Christie et al., 2003; Mann, 1988; Norderhaug et al., 2005).

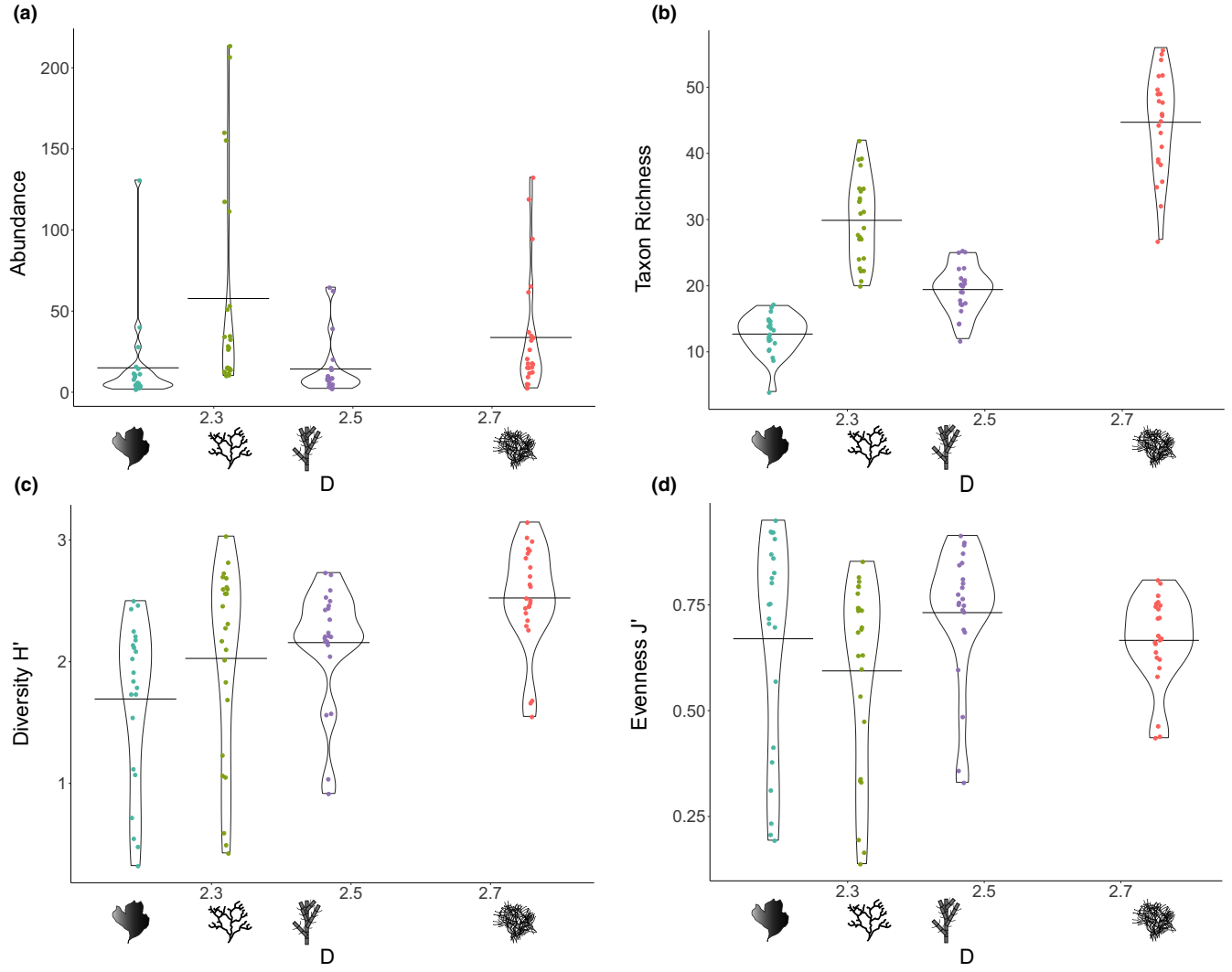

FIGURE 6 Relationship between fractal dimension (D) and macrofaunal abundance (a), taxon richness (b), diversity (Shannon–Wiener *H′*) (c), and evenness (Pielou *J′*) (d) associated with ASU functional groups (left to right: foliose, corticated, ACA and finely branched). Violin plots include the mean (horizontal line) and distribution of the data. All measures of diversity are standardized by ASU volume

While overall the ASUs supported a rich and diverse fauna, our results demonstrated complex interactions between ocean climate, wave exposure and habitat complexity which all had important roles in structuring macroinvertebrate assemblages. While complex, clear patterns were discernible with some taxa having clear thermal affinities leading to different assemblage structure between cold and warm regions. Overall, thermal patterns were driven by a few taxa such as the gastropods *Margarites helicinus* in the cold region and *Tricolia pullus* in the warm region. The regional affinity exhibited by these species was well aligned with their documented thermal distribution (Hiscock, Southward, Tittley, & Hawkins, 2004). An elevated abundance of amphipods and bivalves in the cold region and an increase in decapods and polychaetes in the warm region were also observed. These patterns were comparable, although stronger, than those found in holdfast associated macrofaunal communities across the same study area (Teagle et al., 2018).

Ocean climate also had an influence on macroinvertebrate diversity and abundance with higher macrofaunal abundances at cold exposed sites and more diverse and even assemblages in the warm region. While numerical abundance is not as robust a measure as biomass when considering food web dynamics, these differences are likely to be ecologically significant, since greater macroinvertebrate abundance suggests a larger number of potential prey items which may lead to increased predator abundance. Interestingly, observations of fish assemblage structure along the same gradient indicated a greater abundance of *Pollachius* spp. in the cold compared to warm region with amphipods, which were more numerous in the cold region, dominating their diet (M. Bué et al. unpublished). In the warm region, where macroinvertebrate diversity was highest, fish diversity was also found to be high (M. Bué et al. unpublished). It is possible that the greater number of predator guilds is linked with higher macroinvertebrate diversity in the warm region, as strong predation has been shown to maintain macrofaunal communities below

their carrying capacity, leading to decreased competition for food and space resulting in more diverse communities, which ultimately attract new predators (Dodson, 1970; Menge & Sutherland, 1976; Paine, 1966, 1971). Thus, the thermal affinity of kelp-associated macroinvertebrates observed in our study could be a driver of variation in the wider food web by influencing fish assemblage structure and abundance. However, other factors such as biogeographic affinities of the fish species themselves, localized fishing pressure and habitat availability may also be important and warrant further investigation.

There was also clear evidence of the role of wave exposure in structuring macroinvertebrate assemblages. In terms of abundance and diversity of macroinvertebrates, abundances were higher at cold exposed sites while moderately exposed sites, irrespective of region, were generally more diverse and even. Intense wave action generally favours taxa resistant to such hydrodynamic forces (Fenwick, 1976; Jørgensen & Christie, 2003; Waage-Nielsen, Christie, & Rinde, 2003) resulting in reduced diversity as seen in holdfast communities (Teagle et al., 2018) stipe communities (Norderhaug, Christie, Rinde, Gundersen, & Bekkby, 2014) and in our own study.

Our study, like others (Christie et al., 2009; Hooper & Davenport, 2006; Taniguchi, Nakano, & Tokeshi, 2003; Thomaz, Dibble, Evangelista, Higuti, & Bini, 2008), showed habitat complexity (mm to cm) to significantly and positively influence macroinvertebrate richness and diversity leading to altered assemblage structure. Our findings contribute to the body of knowledge showing the significance of habitat complexity in influencing ecological patterns across multiple spatial scales. Predation of macroinvertebrates by wrasse and other fish species is likely an important structuring process in *L. hyperborea* forests with predator avoidance strategies shaping habitat preferences of kelp-associated fauna (Christie et al., 2007). For example, habitat preferences of amphipods have been shown to be driven by the physical structure of the algal host rather than its nutritional value (Norderhaug, 2004) and stable isotope approaches indicate preferred habitat differed from preferred diet (Nordström, Aarnio, & Bonsdorff, 2016; Schaal et al., 2016). By using ASUs, which remove the influence of diet (barring biofilm development on the ASUs during the experiment), our results support these studies in suggesting predator avoidance behaviour may be a key driver of habitat choice. Although macrofaunal abundance has previously been shown to increase with habitat complexity (Norderhaug, 2004; Norderhaug, Christie, & Fredriksen, 2007; Schaal et al., 2016; Taylor & Cole, 1994; Torres, Veiga, Rubal, & Sousa-Pinto, 2015; Warfe, Barmuta, & Wotherspoon, 2008), this relationship was not found in our study. The lack of similarity with other studies is perhaps due to different measures of habitat complexity used across studies. Different groups of organisms may respond differently to changing fractal dimensions (Tokeshi & Arakaki, 2012) and may lead to contrasting patterns of total macroinvertebrate abundance as observed in our study. Fractal dimension is one measure of habitat complexity that has been shown to be effective in describing patterns in marine and freshwater ecosystems, especially for algae (Gee & Warwick, 1994; Hooper & Davenport, 2006; Thomaz et al., 2008). Habitat complexity, however, is a complex concept and measuring it in multiple ways could improve our understanding of the influences of structural complexity on ecological communities (Tokeshi & Arakaki, 2012).

In conclusion, our study showed that the structure of macroinvertebrate assemblages associated with artificial understory algae in subtidal kelp forests varies across multiple spatial scales and is likely influenced by multiple processes. That said, assemblages clearly varied along a gradient of ocean climate, with some taxa exhibiting strong thermal affinities. Using a space-for-time approach, our study suggests that the structure of kelp-associated communities is likely to alter with continued ocean warming. In parallel, complex kelp forest habitats in many regions of the world are being replaced with low structure, mat-like turfs due to climate change and other anthropogenic stressors (e.g., pollution, eutrophication; Filbee-Dexter & Wernberg, 2018). While some studies suggest these turf communities can be comprised of a diverse set of functional groups (Connell, Foster, & Airoldi, 2014), including those used in our study, others have suggested some functional groups (e.g., ACA and corticated macrophytes) should not be considered turf-forming species (Filbee-Dexter & Wernberg, 2018) and there is evidence of some turfs being functionally depauperate (Filbee-Dexter et al., 2016; Gorman & Connell, 2009; Moy & Christie, 2012). Irrespective, our results and others (Matias, Underwood, & Coleman, 2010) show that the loss of functional diversity and/or structural complexity will alter alpha and beta diversity with implications for higher order consumers including species of commercial importance. Our results collectively suggest that as ocean warming continues and where temperate reefs become less complex, there will be widespread shifts in the structure and functioning of seaweed-dominated communities. Our results provide additional evidence to support the need to reduce the multiple stressors affecting kelp forest ecosystems in order to ensure the functions they provide in supporting high levels of biodiversity as well as the goods and services they supply human society are maintained. This is likely to require active management to reduce stressors entering the systems (e.g., nutrients and pollution) as well as measures to restore degraded habitats. To not do so will have implications for kelp forest ecosystems as well as human society.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data will be made available by contacting the corresponding author.

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BIOSKETCH

The research team are interested in how climate change and other anthropogenic stressors are altering the structure, functioning and resilience of shallow-water marine ecosystems. Much of the teams' research focuses on kelp forest ecology. More details on the groups work can be found at: https://mooremarineecologylab.com and https://www.mba.ac.uk/fellows/smale-group.

Author contributions: P.J.M., D.A.S. and M.B. conceived the idea; P.J.M. and D.A.S. undertook the fieldwork; M.B., G.N. and H.M. identified and enumerated all the taxa; M.B. analysed the data; and M.B. and P.J.M. led the writing with all authors contributing to editing and improving the text.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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